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Biophysical drivers of the carbon dioxide, water vapor, and energy exchanges of a short-rotation poplar coppice

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Abstract

We used the eddy-covariance technique to measure the temporal dynamics and the relationships between leaf area index (LAI) and exchanges of carbon dioxide (CO_2), latent heat (LE) and sensible heat (H) in a multi-genotype short-rotation poplar coppice (SRC) located in East-Flanders (Belgium). The study was carried out over four years (2010-2013) corresponding to the first two rotations of the plantation. The net carbon (C) balance during the first two-year rotation was 75.2 (± 4.4) g C m^{-2} in the establishment year 2010 and -95.6 (± 5.9) g C m^{-2} in 2011. After the harvest (second two-year rotation) the coppice was a net source of carbon, 151.0 (± 10.5) g C m^{-2} in 2012, but a sink of -274.6 (± 18.8) g C m^{-2} in 2013. Overall, at the end of the second rotation this SRC, was a net CO_2 sink with a cumulative uptake of -144.0 (± 22.8) g C m^{-2}. The temporal dynamics and the magnitude of the ratio between gross primary production (GPP) and ecosystem respiration (R_{eco}) were similar to a deciduous forest. The evolution of LAI showed values ranging from 0.96 (± 0.4) to 2.0 (± 1.2) and from 5.1 (±1.5) to 4.5 (± 0.84) during the first and the second rotation, respectively. The GPP (measured close to light saturation) was significantly related to LAI (r^2 of 0.76, $p < 0.001$). The cumulative evapotranspiration (ET) measured during the first rotation was 241.7 mm and 349.9 mm for 2010 and 2011 respectively, and 464.6 mm and 372.1 mm for 2012 and 2013. The average value of surface conductance (G_s) was 0.35 mol m^{-2} s^{-1} and 0.24 mol m^{-2} s^{-1} for the foliated and unfoliated periods, respectively. The mean decoupling factors (Ω) were 0.35 and 0.23 for the foliated and unfoliated periods, respectively, indicating that ET was primarily controlled by vapor pressure deficit (VPD) and G_s (a well-coupled system). The mean Priestley-Taylor coefficient (α) was 0.77 and 0.53 for the foliated and the unfoliated periods, respectively. Such low values indicate that ET was significantly lower than the equilibrium evaporation and thus also lower than the ET of a hypothetical reference crop. During the whole experiment only two short episodes of drought were identified when in May-June 2011 and June 2013 the evaporative fraction dropped below 0.4. The analysis of G_s showed a rather low stomatal control (anisohydric stomatal response) that put the poplar SRC at greater risk during severe drought conditions. All the three mentioned parameters related to ET and GPP (G_s, Ω and α) were significantly and positively correlated to LAI (r^2 from 0.14 to 0.2, $p < 0.0001$), suggesting that LAI was the main biophysical driver controlling the carbon and water balances in this bioenergy production system.

1. Introduction

The European Union has set the target of increasing the use of renewable energy sources to at least 20% of total consumption by the year 2020 (EU, 2009). The objective is to reduce the consumption of fossil fuels and thereby reduce CO_2 emissions (Zetterberg *et al.*, 2014). Within the context of the search for renewable energy sources dedicated lignocellulosic crops, as short-rotation coppice (SRC), have a high potential. Indeed, one might expect a considerable increase in the area of these SRC if they are to be used as conventional biofuel for bioenergy production, or for the production of second-generation biofuels (Eisentraut, 2010).Poplar (*Populus spp.*) is one of the genera that currently receives a lot of attention as a very suitable crop for the production of biofuel (Kauter *et al.*, 2003; Aylott *et al.*, 2008, AEBIOM 2012). The carbon (C) uptake by crops is primarily determined by the biology of the vegetation – e.g., leaf area index (LAI), physiological activity, length of the growing season – as well as by the meteorological conditions (Schmid *et al.*, 2000). The gross primary productivity (GPP) is primarily dependent on the photosynthetically active radiation (PAR), in combination with LAI, while ecosystem respiration (R_{eco}) strongly responds to air and soil temperature (Carrara *et al.*, 2004; Baldocchi, 1997; Reichstein *et al.*, 2002). Carbon uptake in SRC is considered to be very sensitive to low water availability (Broeckx *et al*., 2013), and to high temperatures by stomatal (increase of vapor pressure deficit) and non-stomatal control (influencing R_{eco}) (Migliavacca *et al*., 2009). This suggests that SRC plantations could be vulnerable to climate change in regions where water is in short supply (King *et al*., 2013). Moreover, a poplar SRC might be more sensitive to drought than other deciduous and coniferous forests because poplar is a fast-growing species with rather low stomatal control (Pita *et al.*, 2013).

Monitoring the net ecosystem exchange (NEE) of CO_2 (and its partitioning into GPP and R_{eco}) in combination with the fluxes of sensible heat (H) and latent heat (LE) is essential for quantifying the carbon sequestration potential and water use of SRC plantations, as well as for identifying the main environmental and/or biophysical drivers. Several studies on the physiology of SRC and of longer-rotation poplar plantations have already tried to elucidate the environmental controls (e.g., Neumann *et al.*, 1996; Calfapietra *et al.*, 2003, 2005; Zona *et al.*, 2013). Heatwaves can induce a considerable reduction of the net C uptake in longer rotation (twelve-year) poplar plantations, even in the absence of pronounced soil water stress (Migliavacca *et al.*, 2009). On the other hand

in a two-year-old SRC plantation, soil water shortage limited the NEE when the water table progressively decreased and vapor pressure deficit (VPD) became an important control on CO_2 fluxes. By removing the influence of solar radiation on NEE, VPD explained up to 16% of the variability, and water limitation on CO_2 uptake mostly occurred when VPD was >1 kPa (Zona *et al.* 2013).

Here, we present and discuss measurements of CO_2 and H_2O fluxes in combination with measurements of LAI of a poplar SRC over a four-year period. We hypothesize that LAI explains most of the variability of the eco-physiological parameters that drive the CO_2 and water vapor exchanges. The knowledge of LAI is therefore useful to determine carbon uptake and water use of poplar SRC under various environmental conditions. In terms of water consumption of the SRC crop we hypothesized that the ET of the poplar plantation was lower than the ET of an hypothetical reference crop. The objectives of the present study were: (i) to quantify the magnitude and the seasonal dynamics of CO_2, water vapor and energy exchanges during two two-year rotations for a poplar SRC; (ii) to investigate the role of LAI in controlling GPP and ET; (iii) to quantify and analyze the seasonal variation of surface conductance (G_s), decoupling factor (Ω), and Priestley-Taylor coefficient (α). These latter variables represent important bulk parameters that treat the soil and the vegetation as one single layer, in relation to LAI.

2. Material and Methods

2.1. Site description

The research site was an operational multi-genotype SRC plantation of poplars located in Lochristi, East-Flanders (Belgium; 51°06'44" N, 3°51'02" E) at an elevation of 6.25 m above sea level. The SRC culture was planted on 7-10 April 2010 with 12 selected genotypes of *Populus deltoides*, *P. maximowiczii, P. nigra, and P. trichocarpa,* and their interspecific hybrids in a double-row design with a planting density of 8000 plants ha^{-1}. No fertilizers and no irrigation were applied during the four years of the study. The aboveground biomass was harvested in January-February 2012 (end of the first rotation) and in February 2014 (end of the second rotation). The first rotation was characterized by single-stem plants, while the second rotation consisted a multiple-stem coppice. More details on the planting materials, and on the

plantation lay-out and management are provided by Broeckx *et al*. (2012) and Verlinden *et al*. (2013).

The present contribution and the SRC plantation are part of the larger POPFULL project (http://uahost.uantwerpen.be/popfull) where the full balances of greenhouse gases, of energy and the economics are being evaluated. The 30-year average annual temperature and precipitation (collected by a nearby station of the Royal Meteorological Institute of Belgium; www.meteo.be) at the site are 9.5°C and 726 mm, respectively. The precipitation is equally distributed across the year. The site is characterized by two different former land-use types: extensively grazed pasture, and agricultural cropland (ryegrass, wheat, potato, beet, and most recently monoculture maize with regular nitrogen (N) fertilization at a rate of 200-300 kg ha^{-1} yr^{-1} as liquid animal manure and as chemical fertilizer).

Prior to planting a soil survey (described in detail by Broeckx *et al*., 2012) revealed that the soil has a sandy texture with a clay-enriched deeper soil layer and poor natural drainage. The carbon (C) and N mass fractions were significantly different in the upper 0-15 cm soil layer ($p = 0.0001$) and were lower in previous cropland (1.48% ± 0.32 and 0.12% ±0.03, respectively) as compared to previous pasture (1.95% ± 0.36 and 0.18% ± 0.03, respectively). The C and N contents – in the upper 90 cm – were not significantly different between the two different former land-use types (Broeckx *et al*., 2012).

2.2. Flux and meteorological measurements

The eddy-covariance (EC) system – used to measure gas and energy fluxes between the SRC plantation and the atmosphere – has been extensively described previously (Zona *et al*., 2013). Briefly, the EC system included a three-dimensional sonic anemometer (Model CSAT3, Campbell Scientific, Logan, UT, USA) to measure the wind speed component fluctuations, and a closed-path differential infrared gas analyzer (LI-7000, LI-COR, Lincoln, NE, USA) for the measurements of the CO_2 and H_2O mole fractions in air. Both instruments sampled variables continuously with a frequency of 10 Hz. The sonic anemometer and the inlets of the sampling lines were situated at 5.8 m above the soil surface during a first period (from 1 June 2010 to 30 August 2011), and were raised to 6.6 m thereafter (from 31 August 2011 to 31 December 2013) to match the rapid growth of the plantation. A vacuum pump positioned at the outlet of the LI-

7000 gas analyzer, generated a flow rate of about 20–22 l min^{-1}. This maintained a turbulent flow regime in the sampling line – as required by standard EC methodology – to avoid concentration dilution in the air samples between the sampling line inlet and the gas analyzer, and the consequent, high-frequency fluctuation dampening (Munger *et al*., 2012). To eliminate the fluctuations caused by the pump two buffers (volume of 0.5 l each) were positioned between the pump and the outlet of the analyzer. The sampling tubes were heated and thermally insulated from the environment to prevent condensation and deliquescence of the air samples in the inlet tubes. These phenomena can cause dampening of the water vapor high frequency fluctuations possibly leading to large underestimates of the LE fluxes (Fratini *et al.*, 2012).

Several environmental variables were continuously recorded. Volumetric soil water content (SWC) was measured horizontally in the soil layers 0–30 cm, 0–20 cm, 0–10 cm, and horizontally at specific depths of 1 m, 60 cm, 40 cm, 30 cm, and 20 cm below the surface, using moisture probes (TDR model CS616, Campbell Scientific, Logan, UT, USA). Soil temperature was recorded by temperature probes which provided the average temperature of a soil layer of 8 cm depth (model TCAV-L averaging thermocouples, Campbell Scientific, Logan, UT, USA). Soil heat flux (G) was measured by eight heat flux plates (HFT3, REBS Inc., Seattle, WA, USA) installed at 6-8 cm depth. Air temperature and relative humidity were recorded on the EC mast using a Vaisala probe (model HMP45C, Vaisala, Helsinki, Finland). The net radiation was measured with a four-component radiometer (model CNR1, Kipp & Zonen, Delft, The Netherlands) to give incoming (S) and reflected (S_r) solar (0.3–3 µm), and incoming (L_d) and outgoing (L_u) longwave (far infrared 4.5–42 µm) radiation. Net radiation (R_n) was calculated retrospectively using the equation:

$$R_n = (S - S_r) + (L_d - L_u) \quad (1)$$

Incoming photosynthetically active radiation (PAR; 400–700 nm) was recorded above the canopy using quantum sensors (LI-190, LI-COR, Lincoln, NE, USA).

2.3 Gap-filling and post-processing

Fluxes of CO_2, LE, and H were calculated using the EdiRe software (R. Clement, University of Edinburgh, UK; www.geos.ed.ac.uk/abs/research/micromet/EdiRe/) from high-frequency data series divided in half-hourly averaging periods. The two-component rotation was applied to set mean lateral and vertical wind velocity components to zero while the time delay between scalar

and vertical wind velocity fluctuations was determined by cross-correlation optimization (Foken *et al*., 2012). The frequency response correction was applied to the EC fluxes following Horst (1997). The WPL H_2O vapor correction term of Webb *et al.* (1980) was applied to all the data collected. A filter rejected data using the following criteria: (i) more than ten standard deviations from the 30-minute mean for CO_2, and for the wind velocity components, u, *v*, and w; (ii) more than one standard deviation for H_2O vapor; (iii) for quality flags 9 as suggested by Foken and Wichura (1996) and Foken et al. (2004). To maximize the data coming from the plantation under study only data with wind direction between 50◦ and 250◦ were used. In order to avoid the possible underestimation of fluxes during stable (non-turbulent) conditions at night, data with friction velocity (u*) below a threshold were treated separately using the procedure described by Reichstein et al. (2005). The u* values adopted for each year were 0.15 m s^{-1}, 0.13 m s^{-1}, 0.18 m s^{-1} and 0.2 m s^{-1} for the datasets of 2010, 2011, 2012 and 2013, respectively. A storage term – about 3.4%, 3.8%, 3.1% and 3.7% of the cumulative NEE in 2010, 2011, 2012, and 2013, respectively – was added to the CO_2 flux calculation before setting the u_* thresholds. To follow the rapid changes in canopy height, that characterized the SRC plantation, the displacement height and the roughness length were calculated following the methodologies presented in Arya, (1998) and Stull, (1988).

To estimate the 30-min values of ecosystem respiration (R_{eco}) and GPP, we used the Marginal Distribution Sampling (MDS) method (Reichstein *et al.*, 2005) implemented in www.bgc-jena.mpg.de/~MDIwork/eddyproc/ (2013 version). This method was adopted by the FLUXNET community as a standardized gap-filling and flux-partitioning technique (Moffat *et al.*, 2007; Papale *et al*., 2006). The fluxes of CO_2, H and LE were gap-filled to calculate the cumulative net ecosystem production (NEP) and respective energy balance components with the error propagated from the half-hourly averaged data into the annual uncertainties. To assess the consistency of the EC measurements, we analyzed the linear regression between the half-hourly sum of LE and H, measured by the EC system, versus the difference between R_n and G, obtained with independent measurements. Heat storage in the biomass, in the air column below the EC system and in the soil above the soil heat flux plates was not considered in this analysis.

To determine the relative contribution of the carbon exchange processes to the total exchange we used the ratio GPP/R_{eco}. Values of GPP/R_{eco} less than unity indicate that the crop is a source of

carbon, while values of unity indicate the crop that is carbon-neutral (NEE = 0). When GPP exceeds R_{eco} ($GPP/R_{eco} > 1$) the ecosystem is storing carbon (Falge *et al.*, 2002).

The energy partitioning and the impact of dry periods were evaluated using the evaporative fraction (EF) approach. The instantaneous EF (dimensionless) was calculated from the LE and the H fluxes values as follows:

$$\mathrm{EF}_{\mathrm{daytime}} = \frac{\int_{t1}^{t2} LE(t)dt}{\int_{t1}^{t2}[H(t) + LE(t)]dt} \quad (2)$$

where the time difference t_2–t_1 refers to the time from 11:00 to 14:00 (UTC + 1) in the present study. The growing season was defined as the months with net carbon uptake.

2.4. Plant and leaf area index

Plant area index (PAI) was monitored in 96 plots (i.e., 12 genotypes x 2 former land-use types x 4 replicates), covering the double rows and the space between two adjacent double rows. PAI was measured using the LAI-2000 and LAI-2200 Plant Canopy Analyzers (LI-COR, Lincoln, NE, USA), by comparison of above- and below-canopy readings with a 45^{o} view cap. These indirect PAI measurements were taken from July to November in 2010, from April to November in 2011, from June to November in 2012, and from March to November in 2013. In each plot two diagonal transects were made between the rows, and along each transect measurements were taken with the sensor parallel and perpendicular to the row. Leaf area index (LAI) was obtained by subtracting the woody canopy area index (obtained during leafless periods) from the total plant area index (Wilson et al., 2000). LAI and PAI measurements of the plantation were described and discussed in more detail by Broeckx *et al.* (2014).

To examine the role of LAI in controlling the GPP, and to minimize the confounding effects of varying radiation levels, we analyzed GPP over a narrow range of incident PAR (GPP_{PAR}: GPP when PAR was between 1000 and 1400 µmol m^{-2} s^{-1}) as a function of LAI for each growing season. We also examined the relationships between LE and net radiation, air temperature, and VPD, sorted by two levels of LAI (0-1 and > 4) and tested the influence of LAI using the ANCOVA test.

247 2.5 Surface conductance

248 The surface conductance (G_s, mol m^{-2} s^{-1}) was determined from the rewritten Penman-Monteith
249 equation (Wohlfahrt *et al.*, 2009; Monteith and Unsworth 2013) as follows:

$$G_s = \frac{g_a \gamma}{(1+\beta) + \left(\Delta + VPD\ c_p g_a/(P\ A)\right) - \Delta - \gamma} \quad (3)$$

250

251 with g_a = aerodynamic conductance for heat and water vapor; γ = psychrometric constant; β =
252 Bowen ratio (the ratio of sensible to latent heat flux, or H/LE); Δ = slope of the saturation water
253 vapor pressure curve; VPD = vapor pressure deficit; c_p = specific heat of the air; P = atmospheric
254 pressure; and A = available energy. The available energy was taken as being equal to H + LE,
255 measured by eddy covariance, instead of the measured net radiation minus soil heat flux,
256 throughout the whole study. Two main reasons justified this approach: (i) energy storage into the
257 soil above the heat flux plate(s) as well as storage in the canopy (stem, branches and leaves) and
258 in the air column below the measuring point, which may influence the specific half-hourly
259 energy balance closure, were not quantified; (ii) forcing H and LE to be equal to net radiation
260 minus soil heat flux and closing the energy balance according to the Bowen ratio, generally
261 resulted in a significantly higher noise and unrealistic values of G_s. This Bowen ratio correction
262 is no longer recommended as a universally applicable and a valid solution to a lack of energy
263 balance closure, because there is empirical evidence that most of the missing energy should be
264 assigned to H (Foken *et al*., 2012).

265 The aerodynamic conductance (g_a, mol m^{-2} s^{-1}) was calculated from direct measurements by the
266 EC system according to Liu *et al*. (2007) as:

$$g_a = \frac{\phi_m}{\phi_v}\frac{u_*^2}{u_z} + \frac{6.266}{u_*^{-2/3}} \quad (4)$$

267

268 where ϕ_m and ϕ_v = stability functions for momentum and water vapor transfer; u_* = friction
269 velocity; u_z = wind speed at the reference height z. The righthand side of Eq. (4) expresses the
270 empirically derived excess resistance for scalars relative to momentum (Thom, 1972).

271 The universal stability functions were applied following Dyer (1970) as:

$$\phi_v = \phi_m^2 = \left(1 - 16\frac{z-d}{L}\right)^{-1/2} \quad (5)$$

for unstable conditions and as:

$$\phi_v = \phi_v = 1 + 5.2\frac{z-d}{L} \quad (6)$$

for stable conditions, where d = zero plane displacement, and L = the Obukhov length.

The conversion of g_a from m s^{-1} into mol m^{-2} s^{-1} was made using the combined Boyle´s and Charles´s gas laws (Monteith and Unsworth, 2013).

An estimate of mean stomatal conductance was made following:

$$g_s = G_c/LAI \quad (7)$$

where G_c is the canopy conductance (Lindroth, 1993). Since we did not measure soil and understory LE separately, we assumed that $G_c = G_s$ when the canopy is dry and for LAI > 3 (Herbst, 1995). During these conditions soil and understory LE can be considered as the minor component of LE, although they cannot be completely neglected (Lindroth, 1993).

The physiological control of LE, as compared to the climatological control, was estimated using the Penman-Monteith equation rewritten according to Jarvis and McNaughton (1986):

$$\Omega = \frac{1 + \Delta/\gamma}{1 + \Delta/\gamma + g_a/G_s} \quad (8)$$

where Ω = decoupling factor ($0< \Omega<1$). A value of Ω close to one indicates that LE is mainly controlled by the available energy; a change of G_c results in a very small change of LE (i.e. a de-coupled system dominated by climatological control). In contrast, a small Ω value (close to 0) indicates that LE is mainly controlled by VPD and G_c (i.e. a well-coupled system with a physiological control dominating). In our study we chose the equilibrium LE as the reference representing the evaporation from a wet surface without any advective influences. The ratio between LE and its equilibrium rate can be described in the following form:

$$\alpha = LE/\frac{\Delta\, A}{\Delta + \gamma} \quad (9)$$

where α is the so-called Priestley-Taylor coefficient (Priestley and Taylor, 1972). The deviation of α from unity suggests either well watered conditions with LE enhanced by advective processes ($\alpha >1$) or water-limited ($\alpha <1$) conditions.

The half-hourly values of G_s, Ω, and α were eliminated only for conditions with dry canopy and integrated into daily means weighted by R_n (Wilson *et al*., 2000). The canopy was considered as dry when the amount of intercepted water from precipitation or potential dew condensation was

exceeded by the cumulative equilibrium evaporation. Therefore the interception capacity (mm) was considered to be equal to 0.2 of LAI (Iritz *et al*., 2001).

3. Results

3.1. Meteorological conditions and LAI development

The evolution of the mean daily SWC (in %) along with the water table depth is shown in Fig. 1 panel A: SWC followed the variations in water table depth throughout the entire duration of the study. Precipitation (Fig. 1, panel B) was 556 mm in 2010 (only from June to December), versus 718 mm in 2011, 857 mm in 2012 and 947 in 2013 (entire years), respectively. Precipitation during the period June – September was 355 mm in 2010, 334 mm in 2011, 299 mm in 2012 and 407 in 2013. The average daily air temperature (Fig. 1, panel B) during the period June - September ranged between 18°C and 22°C in all four years. The seasonal dynamics of the daily average R_n were similar in all four years (Fig 1, Panel C).

Although the environmental conditions were rather similar during the four years of the study, the LAI development (Fig. 1, panel D) showed a remarkable difference between the first rotation (2010 and 2011) and the second rotation (2012 and 2013). During the first rotation LAI reached values from 0.96 (± 0.4) in August 2010 to 2.0 (± 1.2) in October 2011. During the second rotation the multiple-stem coppice culture reached values of 5.1 (±1.5) in September 2012 and 4.5 (± 0.84) in August 2013.

3.2. Temporal dynamics of CO_2 and ET fluxes

The net carbon balance during the first rotation was 75.2 (± 4.4) g C m^{-2} in 2010 (from June to December), and -95.6 (± 5.9) g C m^{-2} in 2011. After the harvest (second rotation) the net carbon balance was 151.0 (± 10.5) g C m^{-2} in 2012 and -274.6 (± 18.8) g C m^{-2} in 2013. Considering the two two-year rotations of the SRC plantation together the overall carbon balance was -144.0 (± 22.8) g C m^{-2}. The average rate of carbon uptake during the growing season was -39.6 (± 16.4) g C m^{-2} per month during the first rotation and -59.6 (± 42.5) g C m^{-2} per month during the second rotation. The plantation was also characterized by a different length of the growing season within the same rotation. In 2010 and 2011 (i.e., first rotation) the growing season was from August to September, and from April to September respectively. In 2012 and 2013 (i.e., the second rotation) the growing season was from June to August 2012, and from April to October 2013,

respectively (Fig. 2). The vegetation started later in the first year of each rotation because the crop had to get started either from the woody cutting (first rotation) or from the harvested stem (second rotation).

The GPP/R_{eco} ratio exceeded 1 during the months with a net carbon uptake: considering the two rotations together GPP/R_{eco} exceeded 1 from May to September, and ranged from 1.3 (± 0.36) in May to 1.7 (±1.0) in July (Fig. 3). Annual GPP/R_{eco} values were 0.88 in 2010, 1.07 in 2011, 0.91 in 2012 and 1.35 in 2013.

The cumulative ET measured during the first rotation was 241.7 mm and 349.9 mm for 2010 and 2011, respectively, while during the second rotation, ET was 464.6 mm and 372.1 mm for 2012 and 2013, respectively. During the 2010 growing season ET increased gradually from 1.7 (± 0.47) mm d^{-1} in mid-June to 3.42 (± 1.1) mm d^{-1} in mid-July following the rapid canopy development. In the following year (2011) the rapid increase of ET from 0.33 (± 0.2) mm d^{-1} observed at the beginning of March 2011 to 2.1 (± 1.0) mm d^{-1} at the end of June 2011 was consistent with the rapid increase of the available R_n and with the increasing LAI from 0.62 (± 0.3) in March 2011 to 1.33 (±0.7) in June 2011. A similar pattern was observed in 2012, and in 2013, i.e., during the second rotation. The difference in length of the active growing season was mainly determined by differences in the LAI initiation: e.g., in 2013, the plantation reached an LAI of 2.4 on DOY 151, while in 2012 a similar LAI was reached only on DOY 189. Due to the larger LAI (after coppicing as compared to the two years before coppicing) the growing season ET was constantly higher compared to the previous years before the coppicing (Fig. 4, panel A). Unlike the other growing seasons, in 2012 the plantation was coppiced during the previous winter (in February 2012); this affected the microclimate at the plantation. Throughout the entire spring of 2012 there was only bare soil with stumps covered by the debris of branches and woody chips left after the harvest. As a result, ET was mainly dominated by soil evaporation with lower values measured in March and April 2012 (i.e., 14.1 and 33.2 mm per month) as compared to the same period in 2011 (values of 21.8 and 53.1 mm per month in March and April, respectively; Table 2). In May 2012 the stumps started to resprout, characterized by a very fast growth rate of the stems (with an average of ~10 shoots per coppiced stool) and of the LAI. A consistent observation in each year was the rapid decline in ET related to the canopy senescence starting in September till the end of the season. The overall closure of the surface energy balance was on average 0.68. More specifically, for the 2010 growing season, it was 0.71,

while for the other three growing seasons it ranged from 0.67 in 2011 and 2013 to 0.70 in 2012. The temporal variation of the energy balance closure indicated a higher energy balance closure in the middle of the growing season as compared to the winter periods (Fig. 4, panel C). The lack of energy balance closure may indicate that the absolute values of ET were slightly underestimated. The temporal dynamics of the EF showed a clear seasonality in the energy partitioning (Fig. 4, panel B). The conversion of available energy was favoring LE in spring, summer and autumn, while during winter most of the available energy was partitioned into H.

The maximum EF between 0.8 and 1 coincided with the maximum LAI and indicated that most of the available energy was converted into LE at that time. In May–July 2011 and in June–July 2013, we observed a consistent reduction of the EF, i.e., an increase of H and of the Bowen ratio. This reduction was most probably caused by the lowering of the SWC. The EF did not show a relevant diurnal trend: median values ranged from 0.6 to 0.72 from 09:00 to17:00 (UTC + 1) (Fig. 5). The magnitude of the EF indicates that the plantation did not suffer from severe, or prolonged, periods of drought during the growing season (with the exception of the short periods of May-June 2011, and of June 2013).

3.3 Role of LAI in controlling GPP, LE, and G_s

The relationships between LE and net radiation, air temperature and VPD at different values of LAI are presented in Fig. 6. The analysis of covariance (ANCOVA) revealed a significant effect of LAI on LE, after removing for the effect of net radiation, F (1,1246)= 249.3 , p <0 .05, as well as after removing for the effect of air temperature $F(1,1246) = 5.79$, $p < 0.05$, and VPD $F(1,744)= 82.8$, $p < 0.05$. Statistical parameters of the regressions shown in Fig. 6 are summarized in Table 1. Beside the significantly different slopes, the coefficient of determination of the relationships between LE versus net radiation, air temperature and VPD was always higher for the values with LAI > 4 as compared to values with LAI between 0 and 1. This indicated that LE from the well-developed canopy was generally not only higher, but also less variable in relation to climatological variables as compared to the LE from the sparse canopy which was dominated by the soil and understory LE.

The temporal variation of G_s, α, and Ω showed pronounced seasonal patterns (Fig.7). As expected these three bulk parameters were positively and significantly correlated (Fig. 8). The increase of LAI was accompanied by an increase in Gs. Nevertheless, there were some occasions

when G_s declined despite an increasing LAI; these were associated with short periods of drought. This was most pronounced in May 2011 when LAI development was significantly inhibited. During the periods with low LAI, G_s was mainly driven by (i) soil evaporation which was strongly dependent on surface soil moisture and thus on the distribution and the magnitude of precipitation (Figs. 1 and 7); and (ii) understory transpiration dependent on the density and the species composition of the weed vegetation, its phenology and physiological activity. The average values of G_s were 0.35 mol m^{-2} s^{-1} and 0.24 mol m^{-2} s-1 for the foliated and the unfoliated periods, respectively. The mean Ω was 0.35 and 0.23, and the mean α was 0.77 and 0.53 for the foliated and the unfoliated periods, respectively.

The relationship between the GPP_{PAR} and LAI was well described by a three-parameter exponential function (Fig. 8, panel A). Until LAI reached 2 the relationship appeared to be nearly linear with a mean slope of 8.8 μmol m^{-2} s^{-1} per unit of LAI. For larger LAI values the relationship asymptotically approached the maximum around 30 μmol m^{-2} s^{-1}. The intercept of GPP_{PAR} (equal to 5 μmol m^{-2} s^{-1}) suggests the contribution of weeds to the CO_2 uptake. In contrast to GPP, surface conductance showed a much weaker relationship with LAI (Fig. 6, panel B). In addition, this relationship showed a less asymptotic behavior which may indicate a slight reduction of the water use efficiency when LAI reached the inflection point of the GPP vs. LAI relationship, which was close to an LAI of 2. Similar non-linear relations were found for α and Ω (Fig. 6, panels C and D, respectively). The mean slope of the relationship between G_s and LAI (Fig. 8, panel B) suggests that an increase of LAI by 1 m^2 m^{-2} caused an increase of G_s by 0.043 mol m^{-2} s^{-1}. However, the first half of this increase is determined by the mean slope of 0.061 mol m^{-2} s^{-1} and is reached at an LAI of 2.2. The second half of this increase is characterized by a less steep slope of 0.029 mol m^{-2} s^{-1}. In the case of α, the mean slope was 0.09 per 1 m^2 m^{-2} of LAI with a slightly more pronounced asymptotic limit for higher LAI values. The first half of the α versus LAI relationship was reached at an LAI of 2.1 and was characterized by a slope of 0.14, while the second half was characterized by a slope of 0.05 only. The non-linear, positive relationship between Ω and LAI was described by a mean slope of 0.028. The first half of this increase reached before LAI of 2.1 was characterized by a slope of 0.045, and the second half by a slightly less steep increase of 0.017 per 1 m^2 m^{-2}. When related to LAI all of the four investigated variables (GPP_{PAR}, G_s, Ω and α) showed a departure from the main trend during the drought episodes in May-June 2011 and in June 2013 (Fig. 9).

Light saturated (incident solar radiation > 500 W m^{-2}) g_s, estimated from the EC measurements, showed a strong negative relationship with VPD; this relationship was well described by an exponential decay function $g_s = g_{sref} - m \ln VPD$ (Oren et al., 1999) (Fig. 10, panel A). The reference stomatal conductance (g_{sref}) is the g_s at a VPD of 1 kPa and is represented by the intercept of this function, i.e., 0.12 mol m^{-2} s^{-1}. The parameter m representing the so-called stomatal sensitivity was equal to 0.055 mol m^{-2} s^{-1} $\ln(kPa)^{-1}$. The ratio between m and g_{sref} provides an empirical hydraulic conductivity parameter, and was equal to 0.45 $\ln(kPa)^{-1}$. Values of g_s close to the maximum g_s occurred during conditions of high relative humidity. Measurements during such periods are inherently prone to errors in the EC water vapor flux measurements and to errors in the measurements of VPD itself (by capacitance hygrometers). We therefore excluded the values with a VPD below 0.75 kPa and obtained slightly different parameters: g_{sref} = 0.13 mol m^{-2} s^{-1}, m = 0.0629 mol m^{-2} s^{-1} $\ln(kPa)^{-1}$ and the ratio m/ g_{sref} = 0.49 $\ln(kPa)^{-1}$. In the narrow range of VPD between 0.9 and 1.1 kPa (around the reference g_s) g_s showed a significant linear relation with incident solar radiation where the g_s increased by 0.014 mol m^{-2} s^{-1} for every 100 W m^{-2} of incident solar radiation (Fig. 10, panel B).

4. Discussion

Although SRC plantations are managed in a similar way to agricultural crops (e.g., soil preparation, weed control, irrigation, fertilization, etc.) the magnitude and the temporal dynamics of their GPP/R_{eco} are comparable to those of deciduous forests (Fig. 3). In unmanaged ecosystems the balance between respiratory and assimilatory processes is affected by climate change (Houghton *et al.*, 1996). Systematic changes in the length of the growing season (Randerson *et al.*, 1999; Keyser *et al.*, 2000) indicate an extension of the period favorable for assimilation. In an intensively managed crop –as the SRC of this study – the impact of the management on the length of the growing season appears to be more important; as highlighted by the change in length of the growing season after the biomass was harvested (i.e., second rotation; Fig. 2). The LAI values observed in the present study fell within the range of 4–12 for well-established SRC plantations of poplar or willow (Lindroth *et al.*, 1994; Ceulemans *et al*., 1996; Liberloo *et al*., 2006; Petzold *et al*., 2010, Fischer *et a*l., 2013). The development of LAI – and of canopy closure – depends on plant density, genotypic variety, and vitality of the crop; all these depend on the management regime. The high spatial variability of mean canopy LAI

observed was due to the significant genotypic differences in LAI while the difference between the first and second rotation was due to the multiple stems present after the harvest. This spatial heterogeneity of LAI was most probably also responsible for the unexpected increase of aerodynamic roughness with LAI within the particular growing seasons. Similar dynamics of LAI development, with a peak in the last part of the summer, have previously been described for poplar and willow (Lindroth *et al*., 1994; Ceulemans *et al*., 1996; Guidi *et al*., 2008, Fischer *et al*., 2013).

LAI development is inherently related to the partitioning of the available energy, to ET and to the GPP dynamics (Iritz and Lindroth, 1996; Wilson *et al*., 2000, Blanken et al., 2001, Fischer *et al*., 2013). The cumulative ET measured during the first year was similar to that reported by Fischer *et al*. (2013): a value of 259.4 mm yr^{-1} (from the same period of July to December as in our study). In the following years our cumulative ET values were slightly lower as compared to the values reported by Fisher *et al*. (2013) (i.e., 549.2 mm yr^{-1} and 606.6 mm yr^{-1}, respectively). For a *P. tremula* plantation in Germany an ET value of 441 mm yr^{-1} has been reported (Lasch *et al*., 2010), similar to the value of 403 mm yr^{-1} for a *P. tremuloides* plantation in Canada (Black *et al*., 1996). A number of modeling and experimental studies carried out in various countries across Europe have pointed out that the water use by SRC is substantially higher than that of traditional agricultural crops or grasslands (Hall *et al*., 1996, 1998; Allen *et al*., 1998; Perry *et al*., 2001; Petzold *et al*., 2010). At our site the highest ET rates of *ca*. 5 mm d^{-1} were typically recorded during the late spring and summer, i.e., the periods with the highest evaporative demand. If ET is not limited by undeveloped LAI, this coincidence of maximum ET with the highest evaporative demand generally indicates an adequate water supply. These results are similar to peak values of daily ET in July-August (5 to 6 mm d^{-1}) during the second year after coppice at a poplar plantation in central Europe (Fischer *et al*., 2013) and lower than the peak ET values of 8 to 10 mm d^{-1} for poplar SRC in the warmer climatic conditions of Italy (Tricker *et al*., 2009). These two last studies were conducted on monoclonal plantations of *Populus nigra* × *P. maximowiczii* (clone J-105) respectively *Populus x euramericana* (clone I-214), while our site was a multi-genotype plantation characterized by significant genotypic differences in terms of biomass production and LAI (Broeckx *et al*., 2012; Verlinden *et al*., 2013).

The energy balance closure of 0.7 to 0.83 reported here is typical of that observed in many experiments across international EC networks (Wilson *et al*., 2002a). A more pronounced lack of

energy balance closure in winter is most probably caused by an underestimation of the measured LE due to signal attenuation (Fratini *et al*., 2012). It is quite common practice to distribute this residual energy to H and LE according to the Bowen ratio (Shuttleworth, 2007). However, this procedure was later recognized as not generally valid (Foken, 2008). Some studies indicate that the lack of energy balance closure is associated mainly with H transported by large eddies not detectable by the EC method (Mauder and Foken, 2006; Foken, 2008; Ingwersen *et al*., 2011). It is therefore difficult to quantify the final error in our ET measurements due to energy balance closure.

EF is related to the partitioning of the available energy (Crago and Brutsaert, 1996) and has been used as an index of drought (San Miguel-Ayanz *et al*., 2000; Heim, 2002 Schwalm *et al*., 2010). As indicated by the trend and the magnitude of the EF during the growing season we did not observe prolonged periods of drought apart from the two short episodes in May-June 2011 and in June 2013. In a recent meta-analysis to quantify the drought effects on the carbon cycle and on the terrestrial carbon sink (Schwalm *et al*., 2010) a critical value of 0.4 was reported at the time of the heatwave that occurred across Europe in 2003. During the physiologically active periods, the EF in our study averaged 0.65 (± 0.065) and approached or slightly decreased below the critical 0.4 threshold in the late spring drought period of May 2011 and also slightly in June 2013. The diurnal trend of EF showed nearly constant values with only a slight increase toward the late afternoon; this agreed with the daytime self-preservation of the EF assumption (Sugita and Brutsaert, 1991; Brutsaert and Sugita, 1992; Crago and Brutsaert, 1996). However, more recent analyses (Peng *et al*., 2013; Gentine et al., 2011) indicated a consistent daytime trend of the EF.

The relations between g_s, G_c, G_s and VPD and solar radiation, water availability and temperature have been the core of various ecophysiological models (Lindroth *et al*., 1994; Cienciala and Lindroth, 1995; Hall *et al*., 1996; Kim et al., 2008). Since G_c is a product of g_s and LAI, G_c is tightly correlated with LAI or more specifically with its solar equivalent (Čermák, 1989, Kim *et al*., 2008). In the case of G_s, the relationship is hampered by the influence of soil and understory LE. In spite of this soil and understory LE we found a significant relation between G_s and LAI with a mean slope of 0.043 mol m^{-2} s^{-1}, which is consistent with other studies. For instance, Wilson *et al*. (2000) reported the slope of the relationship of g_s versus LAI as 0.63 mol m^{-2} s^{-1} for a mixed deciduous forest, while for an aspen forest with a hazelnut understory a value of 0.048

mol m^{-2} s^{-1} has been reported (Blanken *et al*., 2004). In general, the positive correlation between g_s and LAI is the highest when the soil surface is dry, but there is adequate water available deeper in the root zone. However, under the Belgian climate conditions with a relatively high annual precipitation well distributed over the season, there are hardly any conditions of a dry soil surface over a long period of time.

The average G_s of 0.35 mol m^{-2} s^{-1} during the foliated period in this study is comparable to the average G_s of 0.27 mol m^{-2} s^{-1} for a monoclonal poplar plantation (*Populus nigra x P. maximowiczii*) in the Czech Republic over several growing seasons including one year after coppice with a very low ET (Fischer *et al*., 2012). In an SRC of willow in Sweden G_c values ranged from 0.45 to 1.1 mol m^{-2} s^{-1} (Lindroth, 1993) and these values slightly differed from the maximum G_s of our study that reached 0.76 mol m^{-2} s^{-1} in September 2012. In an attempt to quantify the partitioning of LE and H during the warm season (mid-June to late August) at 27 FLUXNET sites covering a wide range of terrestrial ecosystems, Wilson (2002b) reported a range of G_s values at midday that varied from 0.4 to 0.67 mol m^{-2} s^{-1} for deciduous forests while it was 0.66 mol m^{-2} s^{-1} for a conventional poplar plantation. By comparing our mean G_s of 0.35 mol m^{-2} s^{-1} with the G_s 0.64 mol m^{-2} s^{-1} of the hypothetical reference grass (Allen *et al*., 1998) we can infer that water consumption of our poplar SRC was significantly lower than that to be expected from the reference grass, despite the higher aerodynamic conductance of the aerodynamically rougher SRC.

The average Ω equal to 0.35 indicated a rather good coupling to the atmosphere. This value mathematically means that changing G_s by 10% results in a 6.5% change in LE; thus stomata play an important role in controlling LE. Interestingly, we did not observe a decrease of g_a or u/u_* (data not shown) with an increase of LAI suggesting that this multi-genotype SRC was aerodynamically smoother during the unfoliated periods. This also means that the positive linear relationship between LAI and Ω was mainly due to the significant increase of G_s.

The average value of Ω is consistent with many other studies focusing on poplar or willow SRC: similar results were obtained for a willow stand in southern Sweden with an Ω value of 0.4 (Cienciala, 1994). For a poplar SRC a decoupling coefficient between 0.16 and 0.6 – with an average of 0.41 – was reported and the highest values were associated with the higher LAI values (Fischer *et al.* 2012). Likewise, Lindroth (1993) found that the decoupling coefficient was low (0–0.4) at LAI < 1; afterwards, with increasing LAI, the Ω value increased into the range of

0.6 to 0.8. So, their SRC stand (Lindroth, 1993) was well-coupled to the atmosphere for low values of LAI, and it was practically de-coupled for LAI values above about two. An average Ω of 0.66 was reported for a high-density plantation of hybrid poplars (*P. trichocarpa x P. deltoides*) in the Pacific Northwest (Hinckley *et al*., 1994), which also means a poor coupling to the atmosphere. In contrast, a rather low decoupling coefficient of 0.31 was reported for a boreal aspen (*P. tremuloides*) forest in Canada (Blanken *et al*., 1997). Likewise, values of the decoupling coefficient never exceeded 0.3 for *P. euphratica* grown in a plantation on degraded cropland with increased salinity in Uzbekistan (Khamzina *et al*., 2009).

The mean annual Priestley-Taylor coefficient, α, equal to 0.77 is very similar to the α value of 0.7 reported for a deciduous mixed forest (Wilson *et al.*, 2000) and slightly lower than a Canadian aspen forest with α of 0.99 (Blanken *et al.*, 2004). The average α value of 0.77 also means that the ET of the poplar SRC was 23% lower than the equilibrium ET. This equilibrium is in addition on average 8% lower than the ET of the hypothetical reference grass cover without water and nutrient limitations (Allen *et al*., 1998). This implies that ET of our multi-genotype SRC was, in general, significantly lower than ET of the grasslands confirming the recent findings reported by Fischer *et al*. (2013).

The analysis of the stomatal conductance showed a significant decrease of g_s in response to VPD and an increase in response to solar radiation: these relationships reflect the well-known fact that plants open their stomata when exposed to light and close them when the evaporative demand of the atmosphere is increasing (Lindroth *et al*., 1993; Kim *et al.*, 2008). By doing so plants maximize the carbon uptake while they prevent the decrease of the leaf turgor and xylem cavitation and embolism (Domec *et al*., 2012).

The ratio of m to g_{sref} represents an important hydraulic parameter and indicates whether a particular species is able to maintain a constant minimum leaf water potential (isohydric) via its stomata or has a lower control of its leaf water potential (anisohydric). (Domec et al., 2012). Poplar is known to exhibit the two contrasting hydraulic behaviors (Domec *et al*., 2012; Hinckley *et al*., 1994). The ratio of m to g_{sref} equal to 0.45 mol m^{-2} s^{-1} $ln(kPa)^{-1}$ found in the present study indicates a rather weak stomatal control as compared to a generic value of 0.6 mol m^{-2} s^{-1} $ln(kPa^{-1})$ for isohydric species (Oren *et al*., 1999). Mean leaf-level ratios of m and g_{sref} equal to 0.45 mol m^{-2} s^{-1} $ln(kPa)^{-1}$ based on porometric measurements, and of 0.64 mol m^{-2} s^{-1} $ln(kPa)^{-1}$ based on the sap flow technique, were previously reported for hybrid poplar *(P.*

trichocarpa × *P. deltoides)* by Kim *et al*. (2008). A typical isohydric behavior with mean ratio of m to g_{sref} around 0.62 mol m^{-2} s^{-1} ln(kPa) $^{-1}$ was reported for a mature poplar hybrid (*P. nigra* × *P. maximowiczii*) stand in Germany (Schmidt-Walter *et al*., 2014). The rather lower stomatal control of our multi-genotype SRC is in accordance with previous studies suggesting that this SRC potentially had a higher sensitivity to prolonged drought spells and exhibited a different strategy characterized by leaf abscission rather than by a tight stomatal control (Pita *et al*., 2013). This rather anisohydric behavior may put our multi-genotypic poplar SRC at greater risk of xylem dysfunction in extreme environmental conditions compared to SRC with species characterized by a purely isohidric behavior as e.g., the monoclonal SRC (*P. nigra* × *P. maximowiczii*) presented by Schmidt-Walter *et al*. (2014).

The g_s of 0.13 mol m^{-2} s^{-1} under reference meteorological conditions (VPD of 1±0.1 kPa and incident solar radiation > 500 W m^{-2}) observed in the present study was lower than the g_{sref} close to 0.45 mol m^{-2} s^{-1} reported for a hybrid poplar plantation (*P.* x *canadensis*) in northern Italy (Migliavacca *et al*., 2009). This might be partly explained by differences in LAI. The maximum LAI in the study of Migliavacca *et al*. (2009) was only 2, and thus a relatively larger portion of the canopy was exposed to the incident solar radiation as compared to the maximum LAI values of 3 to 5 observed in the present study. At the same time soil and understory LE still significantly influenced G_s for an LAI of 2, and from that inferred g_s. In contrast, Kim *et al*. (2008) found g_{sref} values within the range of 0.070 to 0.142 mol m^{-2} s^{-1} measured by sap flow and porometer techniques, values that are more consistent with our findings.

Summarizing the relationships presented and discussed, g_s was an important variable that is physiologically related to transpiration and to GPP. The diurnal variation of g_s can be well predicted using the physically based relationships between incident solar radiation and VPD.

5. Conclusion

The SRC plantation examined in this study became a carbon sink at the end of the second rotation. Despite the intensive management, the magnitude and the annual temporal dynamics of the SRC, the GPP/R_{eco} ratio appears to be similar to a deciduous forest. The ET was significantly lower than the equilibrium evaporation and lower than the ET of a hypothetical reference crop; this observation disputes the general perceptions of poplar SRC to be big water consumers. The magnitude and the rapid development of LAI, characteristic for an SRC, was apart from the

meteorological conditions, the main biophysical driver of the seasonal and intra-seasonal variation in carbon uptake and in evapotranspiration. Therefore, we suggest that the GPP_{PAR} and G_s (or alternatively α) could be used as indicators of the carbon uptake and the ET of poplar SRC without water stress wherever the LAI and the common meteorological variables are available. Longer observations should evaluate the full impact of the management and should give more reliable assessments of the water and carbon balances.

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	LAI 0-1					LAI 4-6				
	constant	B	*SE* B	β	R^2	constant	B	SEB	β	R^2
Rg	25.61	0.33	0.01	.79*	0.62	36.71	0.48	0.01	.87*	0.77
Air T	-31.6	6.72	0.55	.35*	0.13	-107.85	12.86	0.6	051*	0.27
VPD	102.12	32.16	6.48	.26*	0.07	131.52	72.75	10.46	.32*	0.10

Table 1 Regression coefficients of the relationship between latent heat (LE) (dependent variable) and net radiation (Rg), air temperature (Air T) and vapor pressure deficit (VPD (predictors) for two levels of leaf area index (LAI).

*$p < .05$

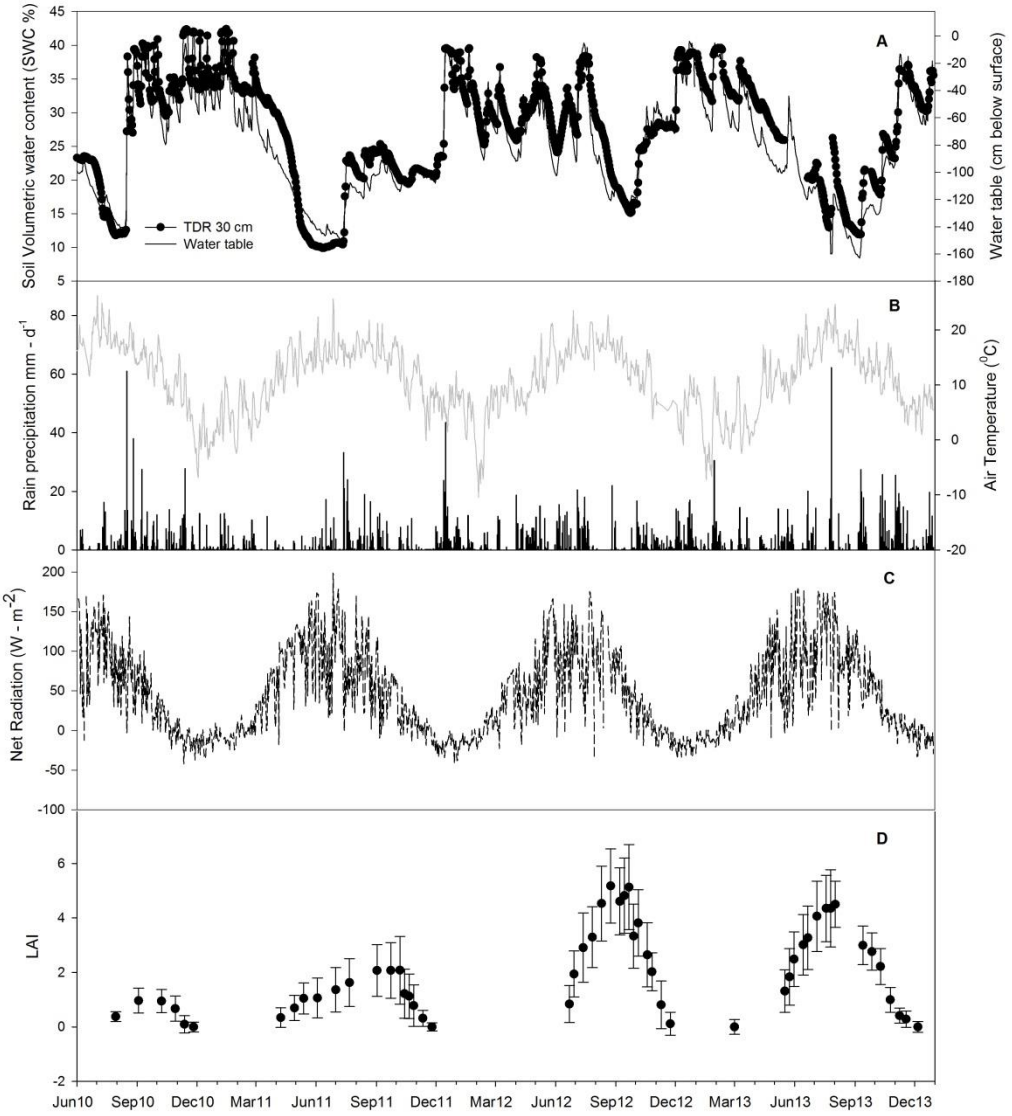

Fig. 1 Evolution of different environmental parameters and leaf area index (LAI) during the course of the four growing seasons of the short-rotation poplar plantation. Panel A: daily average temporal trend of the water table depth and volumetric soil water content (% as measured with TDR. Panel B: mean daily air temperature (^{o}C) and precipitation (mm d^{-1}). Panel C: daily average net radiation. Panel D: seasonal distribution of leaf area index (LAI): measurements (data points) represent the average of the 12 clones of the plantation and vertical bars represent the standard deviation.

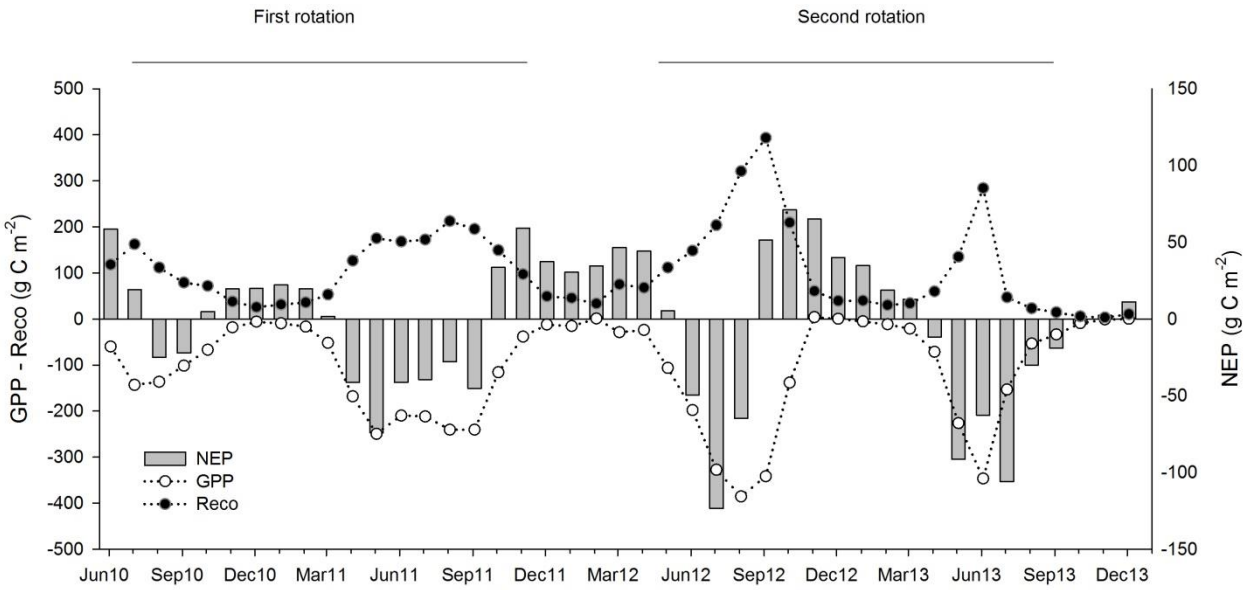

Fig. 2 Seasonal dynamics of the monthly cumulative gross primary production (GPP), ecosystem respiration (R_{eco}) and net ecosystem production (NEP) during the two rotations (four years) of the short-rotation coppice plantation.

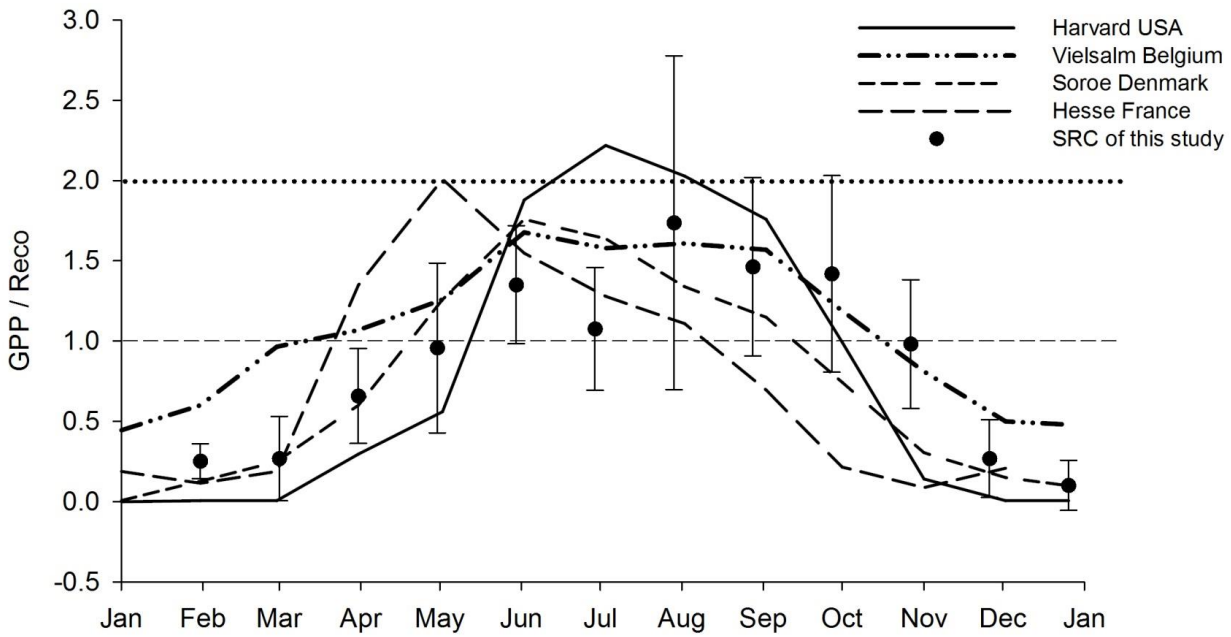

Fig.3 Annual dynamics of the gross primary production and ecosystem respiration ratio (GPP/Reco) at the study site as compared to a series of deciduous forests reported by Falge et al. (2002). An GPP/Reco value of 1 (dashed line) indicates that the cumulative net ecosystem exchange (NEE) was equal to 0. The value of 2 (dotted line) corresponds to the cumulative NEE begin equal to Reco, indicating a low overall contribution of the heterotrophic respiration.

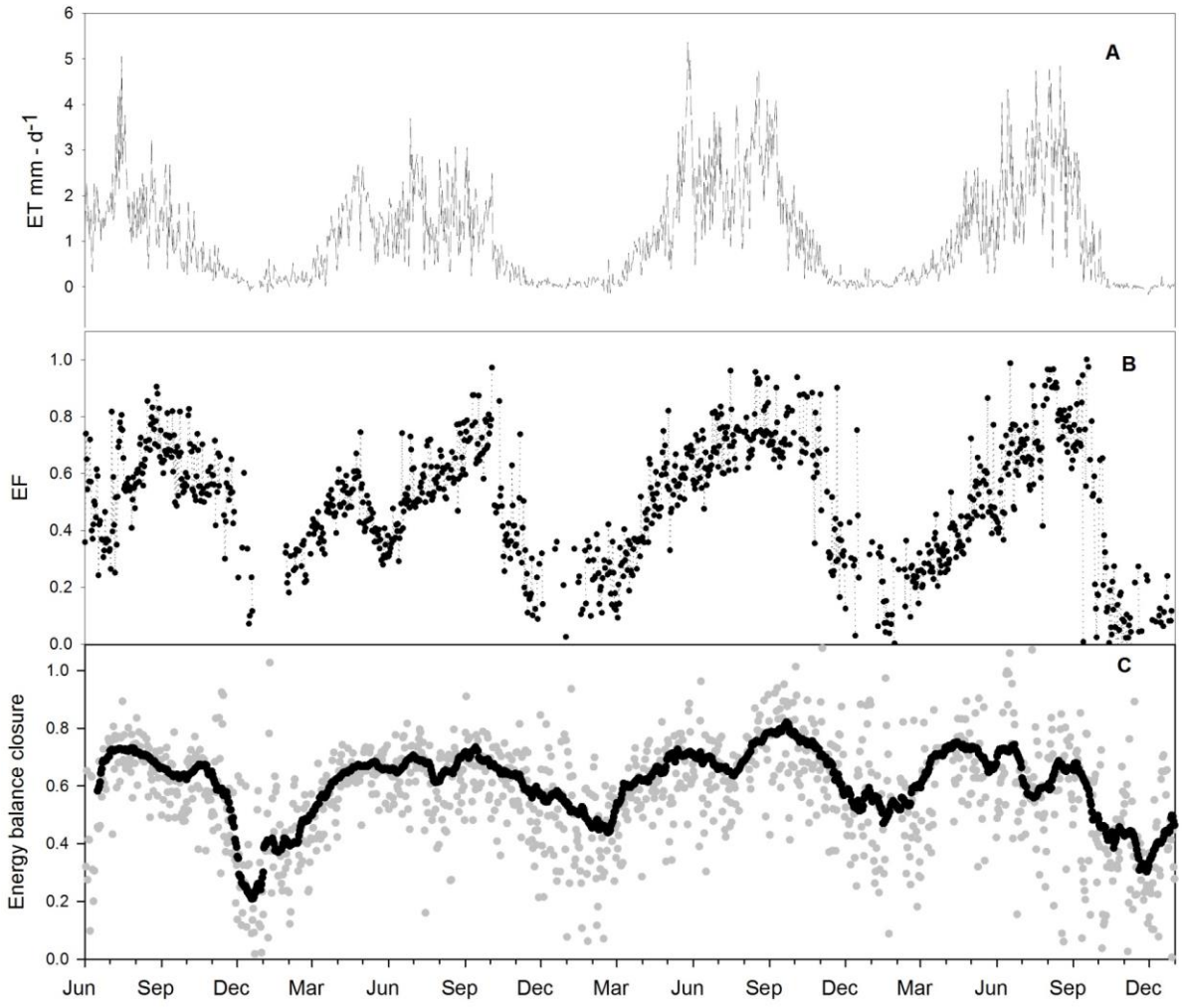

Fig. 4 Panel A: Temporal dynamics of the daily evapotranspiration totals (ET). Panel B: midday average evaporative fraction (EF) as a measure of energy partitioning and as an indicator of eventual drought episodes calculated for midday periods from 11:00 to 14:00. Panel C: temporal variation of the energy balance closure using non-gap-filled data. The gray points represent the daily linear regression slopes of the relationship between available energy (Rn-G) and eddy-covariance energy fluxes (H + LE). The black points represent the slopes of a running window of 30 days. H = sensible heat, LE = latent heat, G = soil heat flux, Rn = net radiation.

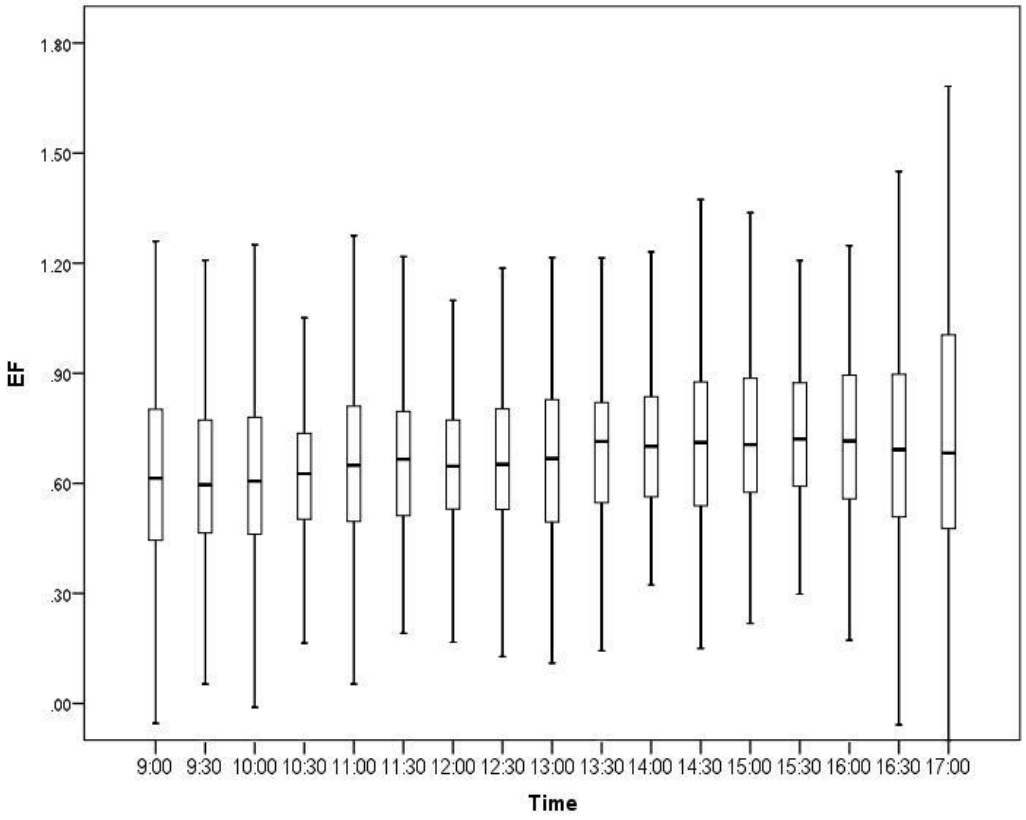

Fig. 5 Box plots of the daily trend of the evaporative fraction (EF) measured during the 2013 growing season. Each box covers the interquartile range (50% of the scores); the median value is drawn as a horizontal black line, and the whiskers indicate the bottom and top quartile.

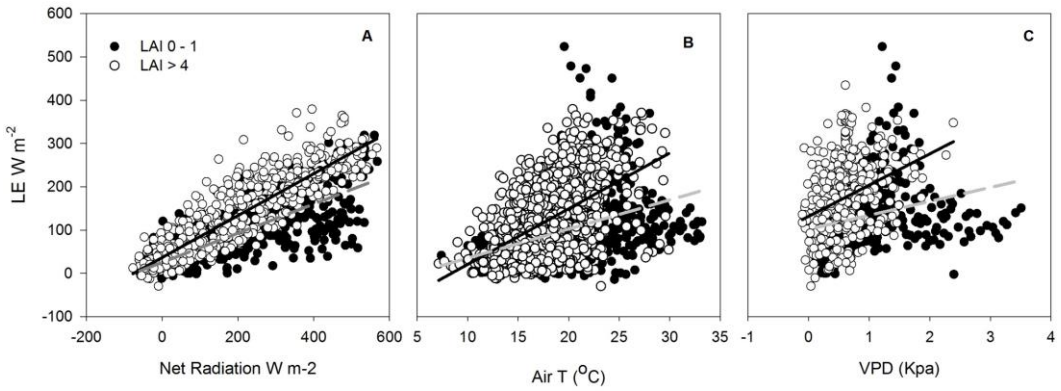

Fig. 6 Relationship between latent heat (LE) and net radiation (R_n; panel A), air temperature (Air T) (panel B) and vapour pressure deficit (VPD; panel C) at two levels of LAI: 0-1 (black circles) and LAI > 4 (white circles). LAI = Leaf area index

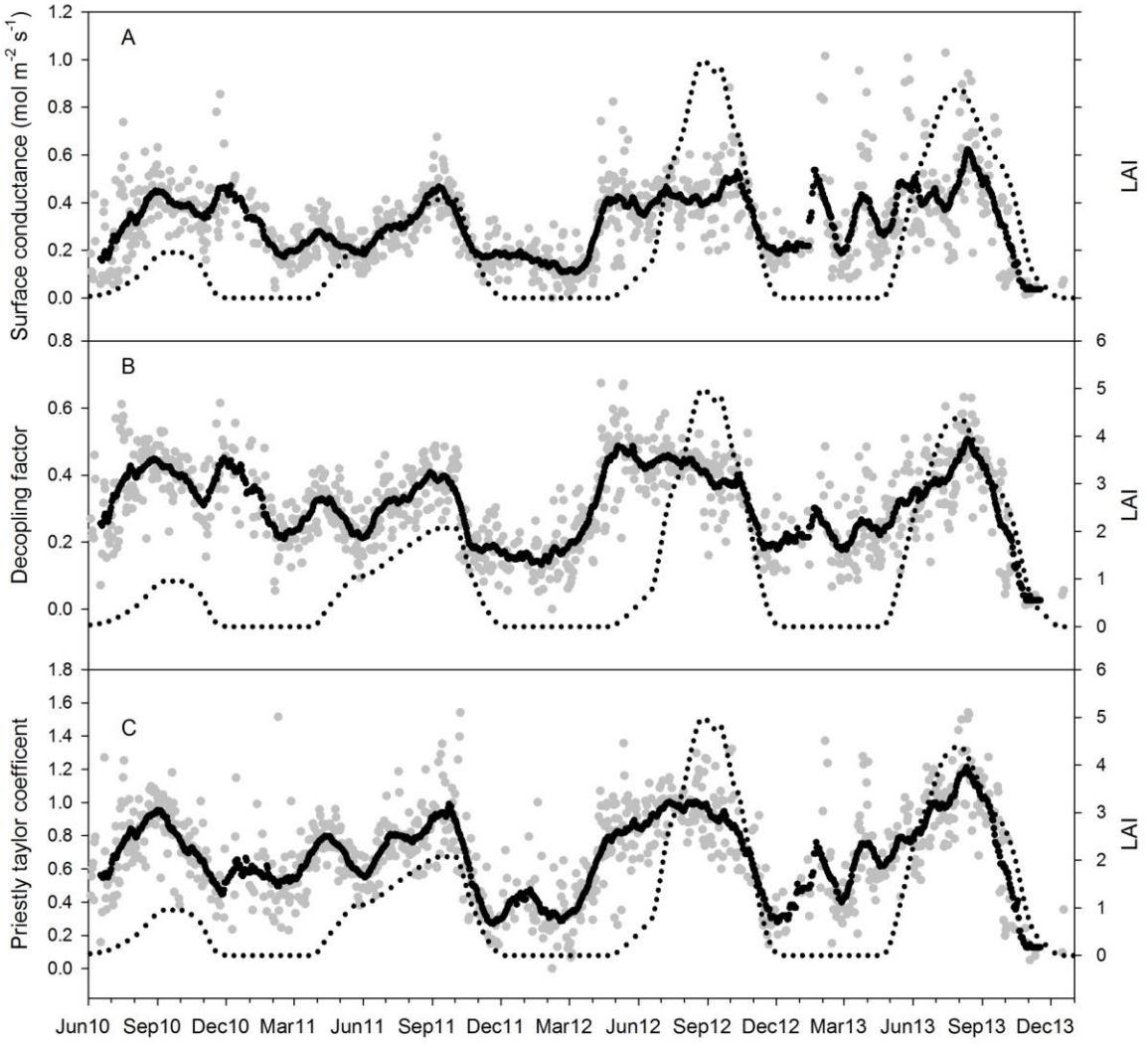

Fig. 7. Temporal variation of surface conductance (A), decoupling factor (B) and Priestley-Taylor coefficient (C) expressed as daily means weighted by net radiation (gray points). Data are calculated from half-hourly diurnal values during conditions with a dry canopy. The days when less than 30% of the diurnal values were available were excluded from the analysis. The black solid line expresses the 30-day running mean calculated from the daily values. The dashed black lines depict the leaf area index (LAI).

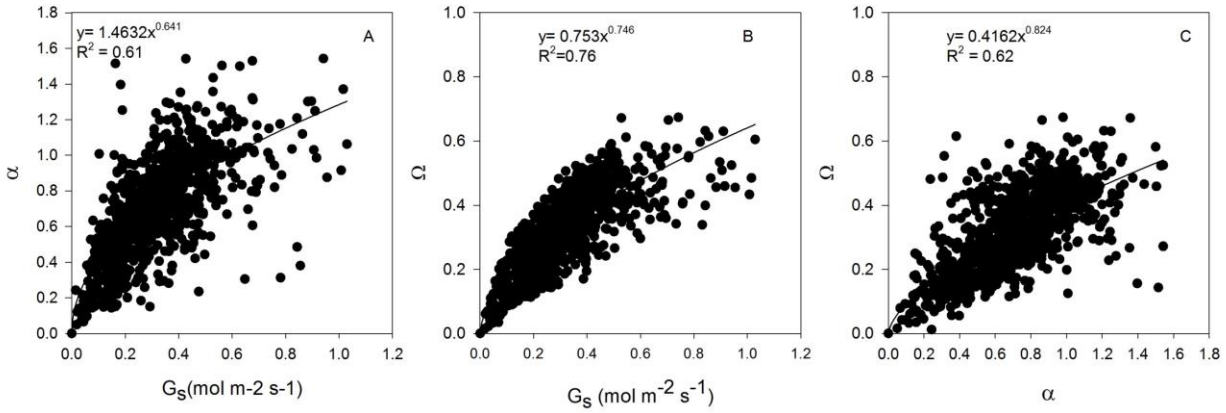

Fig. 8. Scatter plot relationships between surface conductance (G_s) and Priestley-Taylor coefficient (panel A), surface conductance and decoupling factor (panel B), and Priestley-Taylor coefficient and decoupling factor (panel C). The points represent daily means of diurnal values for dry surface conditions weighted by net radiation. The days when less than 30% of diurnal values were available were excluded from the analysis.

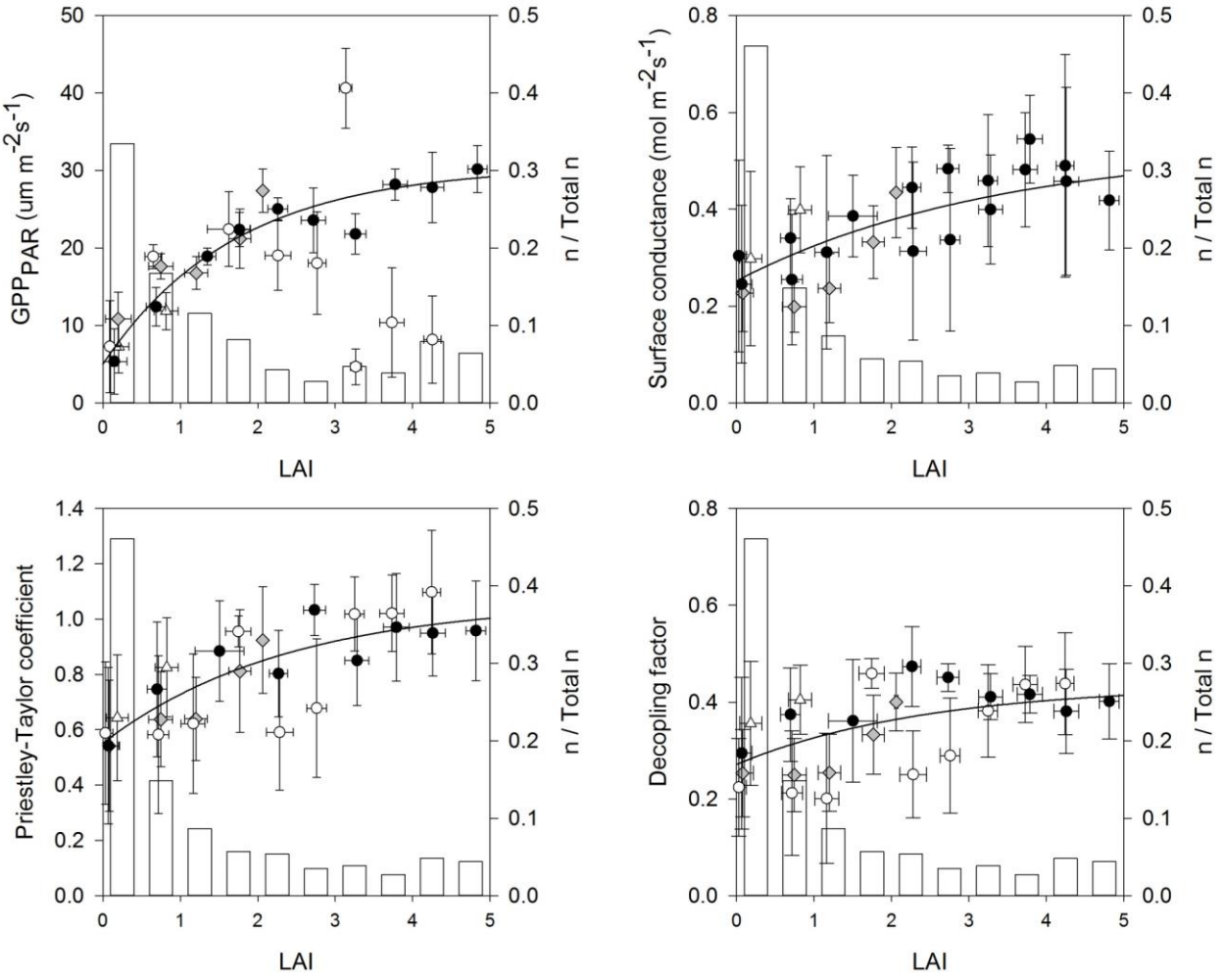

Fig. 9 Relationships between leaf area index (LAI) and gross primary productivity (GPP) described by the function GPP_{PAR}= 30.55-25.52*EXP(-0.58*LAI) R^2 = 0.76 (A); surface conductance and leaf area index described by the function G_s = 0.53-0.28*EXP(-0.3*LAI), R^2 = 0.18 (B); Priestley-Taylor coefficient versus leaf area index described by the function α = 1.06-0.51*EXP(-0.42*LAI) R^2 = 0.30 (C); and decoupling factor and leaf area index expressed by the function Ω = 0.43-0.16*EXP(-0.41*LAI) R^2 = 0.14 (D). All of the parameters were statistically significant ($p < 0.0001$). The points represent the averages of daily values binned according to leaf area index (0.5 m^2 m^{-2}). White triangles: season 2010; gray diamonds = 2011; black circles = 2012 and white circles = 2013. The error lines indicate the standard deviation. The white vertical bars show the frequency distribution. Daily means are calculated from diurnal half-hourly values during conditions with a dry canopy and weighted by net radiation. The days when less than 30% of diurnal values were available were excluded from the analysis. In case of GPP, four distinctive outliers representing 37 days in summer 2013 were excluded for fitting the function.

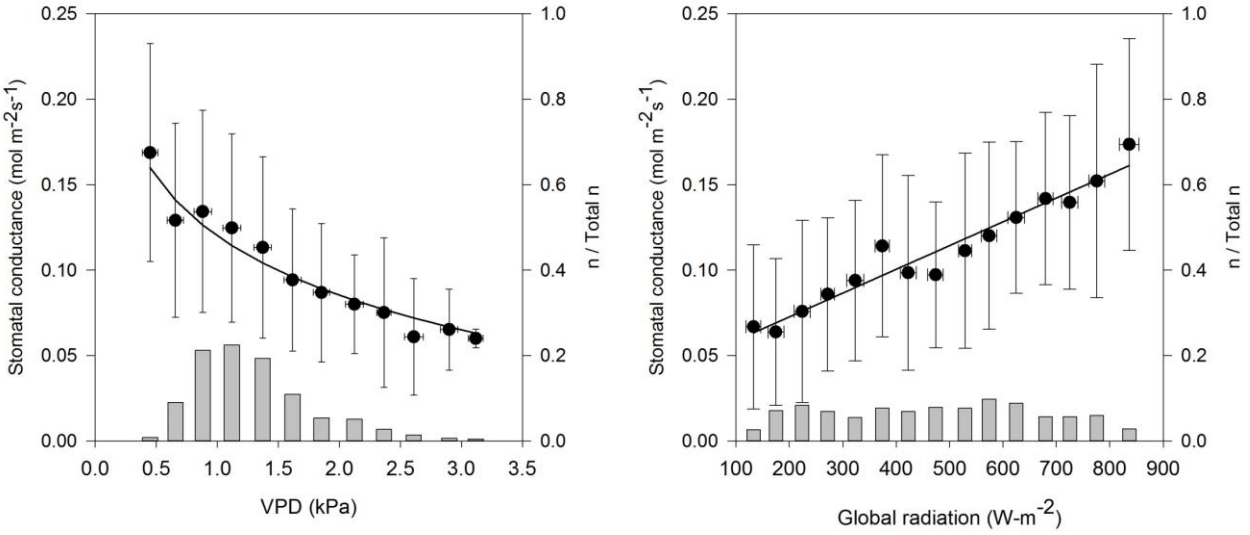

Fig. 10: Relationship between vapor pressured deficit (VPD) and mean stomatal conductance (g_s) for light saturated conditions (global radiation > 500 W m^{-2}) (left panel, A). The particular points express the averages of the half-hour values binned according to VPD (0.25 kPa). Relationship between global radiation and reference mean g_s (right panel, B). Points represent the averages of half-hourly values binned according to global radiation (50 W m^{-2}). The reference mean g_s was calculated in narrow range of vapor pressure deficit between 0.9 to 1.1 kPa. Mean g_s is represented by the surface conductance divided by the leaf area index (LAI) during dry canopy conditions when LAI exceeded 3. The error lines indicate the standard deviation and the gray vertical bars show the frequency distribution.